Evolutionary plant radiations: where, when, why and how?

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Editorial

Evolutionary plant radiations: where, when, why and how?

Radiations generating exceptionally diverse clades are a fundamental component of evolutionary diversification across all organismal groups. For plants, radiations have occurred in many different geographical and ecological settings, many different plant lineages, and at many different times over the last 400 million years. This prevalence means that working out the causes, mechanisms and outcomes of radiations is central to understanding the evolution of plant diversity. This Special Issue of *New Phytologist* focuses on plant radiations and contains 19 papers spanning a vibrant mix of conceptual, methodological and empirical contributions. These papers result from the Symposium, *Plant Evolutionary Radiations: Where, When, Why and How?,* which took place in Zürich (Switzerland), 13–14 June 2014 (http://www.systbot.uzh.ch/static/congresses/radiations/).

The complementary primary data that inform us about evolutionary diversification – fossils and time-calibrated molecular phylogenies – are amply represented in this Special Issue, with landmark studies using either both in combination or just one type of information. Macro-evolutionary studies have proliferated massively in recent years with the development of time-calibrated molecular phylogenies. For the first time these are revealing what had been suspected for a long time: the existence of extensive diversification rate heterogeneity through time, among lineages, and in different geographical and ecological settings. As a result, in the last decade, investigating the patterns and processes of radiations has become both possible and highly topical, and research in this area has been developing very rapidly. This Special Issue summarizes the current state of play about *Where, When, Why and How* plant radiations happened, and the significant progress that has been made over the last few years since these questions were last posed (Linder, 2008).

In light of these advances it is interesting to reflect upon what constitutes a radiation. This is an old and well-trodden debate (Givnish, 1997, in this issue, pp. 297–303; Sanderson, 1998; Donoghue & Sanderson, pp. 260–274) not least because the term radiation can encompass a wide spectrum of concepts. Few would disagree that most radiations involve elements of both adaptive (phenotypic trait or ecological) diversification and lineage (species) diversification (Sanderson, 1998; Donoghue & Sanderson, pp. 260–274; Losos & Mahler, 2010; but see Givnish, pp. 297–303). Some would argue that radiations must constitute rapid episodes of species and/or trait diversification. The ability to quantify rates of evolution and locate rate shifts across phylogenies more precisely (reviewed by Stadler, 2013; Morlon, 2014), opens up opportunities to understand the interplay between species and trait diversification on a scale not previously envisaged (e.g. Venditti *et al.*, 2011; Rabosky *et al.*, 2013). With these more powerful insights come possibilities to define radiations more objectively and quantitatively (e.g. Drummond *et al.*, 2012), but also in more specific and restrictive ways (Bouchenak-Khelladi *et al.*, pp. 313–326; Donoghue & Sanderson, pp. 260–274). This new era of quantitative analyses argues for retaining a broad concept of what constitutes a radiation – as adopted in this Special Issue – whilst recognizing the finer conceptual distinctions, many particular types of radiations (e.g. adaptive radiation, non-adaptive radiation, mixed model radiations, explosive species diversification, super radiation, semi-replicated radiations, progressive radiations, convergent radiations), the potential continuities across these definitional spectra (Olsen & Arroyo-Santos, 2009), and the diverse evolutionary processes underlying radiations (Givnish, pp. 297–303).

Where?

The numerous examples of radiations on islands have been especially influential for understanding evolutionary diversification (Losos & Ricklefs, 2009). Such studies have a long pedigree, and one that is being progressively enriched by the many radiations being documented in other island-like systems, such as mountains and lakes (Hughes & Atchison, pp. 275–282; Seehausen, pp. 304–312). All of these island and island-like systems, are characterized by obvious extrinsic ecological opportunities – the new adaptive zones highlighted by Simpson (1953) as important drivers of radiations. However, it has become ever more apparent that plant radiations are everywhere across the planet in diverse geographical and ecological settings, including most of the world's terrestrial biomes. Plant radiations documented here are found in tropical Amazonian rain forests (Koenen *et al.*, pp. 327–339), north temperate forests (Spriggs *et al.*, pp. 340–354), mountains – both montane forests (Schwery *et al.*, pp. 355–367; Verboom *et al.*, pp. 368–376) and alpine/tropical-alpine grasslands (Hughes & Atchison, pp. 275–282), and Mediterranean vegetation zones (Breitkopf *et al.*, pp. 377–389; Cook *et al.*, pp. 390–400; Reyes *et al.*, pp. 401–410; Verboom *et al.*, pp. 368–376). It seems that the extrinsic circumstances under which radiations occur can be extremely diverse, including supposedly stable environments, such as tropical rainforests, or *fynbos* vegetation in the Cape Floristic Region, where ecological opportunities are harder to demonstrate than on islands and island-like formations. Either the extrinsic opportunities in these environments have yet to be elucidated, perhaps because they are more subtle, patchy or transient, or the expectation of extrinsic opportunity as a requirement for radiation is misplaced. There is still much to do to characterize, quantify and compare extrinsic ecological opportunities and how they have

contributed to radiations (e.g. Wagner *et al.*, 2012; Hughes & Atchison, pp. 275–282). Perhaps the most consistent common thread underpinning radiations are key landscapes (*sensu* Givnish, 1997) with high physiographic (topographic, edaphic, hydrological, habitat) heterogeneity (Verboom *et al.*, pp. 368–376; Schwery *et al.*, pp. 355–367; Spriggs *et al.*, pp. 340–354) and multidimensional environmental gradients (Seehausen, pp. 304–312).

When?

Establishing a robust relative timeframe is critical for assessing variation in rates of species and trait diversification and identifying radiations (e.g. Chomicki & Renner, pp. 411–424). However, when looking for correlates of radiations and assessing whether these coincide, pre- or post-date a radiation (Bouchenak-Khelladi *et al.*, pp. 313–326), an absolute time-frame is needed. In this Special Issue two studies address methodological issues and present new empirical evidence for the timing of diversification of vascular plants (Silvestro *et al.*, pp. 425–436; Niklas, pp. 254–256) and angiosperm families (Magallón *et al.*, pp. 437–453; Sanderson, pp. 257–259). Silvestro *et al.* (pp. 425–436) present the first Bayesian analysis of the diversification dynamics of vascular plants based on macrofossil data at a global scale. Using a large generic level fossil data set and a novel probabilistic approach that takes into account fossil preservation processes, they document major turnover events among the major vascular plant lineages – spore-bearing plants, nonflowering seed plants and flowering plants – more accurately than has been possible up to now. Furthermore, they provide explicit probability distributions for divergence time estimates for these lineages that can be used as calibration priors for dating phylogenies of these clades. Equally notable is the new timeframe for angiosperm diversification, based on a comprehensive rate-corrected phylogeny incorporating the majority of families and time-calibrated using 137 fossils, which provides the most robust estimates of the stem ages of angiosperm families to date (Magallón *et al.*, pp. 437–453). This study suggests that molecular divergence time estimation is becoming more sophisticated and robustly cross-validated. However, it is also clear that there is still some way to go to converge on robust consensus ages of plant taxa. The bias towards overly young divergence time estimates revealed by the treasure trove of plant fossils discovered in Patagonia over the last decade, which are almost all older than the molecular divergence time estimates for their respective groups (Wilf & Escapa, pp. 283–290), comes as a timely warning shot across the bows of the flotilla of published molecular time trees and the sometimes uncritical ways in which fossil priors are used. Rigorous standards in applying fossil priors are far from universal and a more thorough survey and selection of additional fossil constraints, including the new Patagonian fossils highlighted by Wilf & Escapa (pp. 283–290), are needed.

Closer to the present, an on-going proliferation of time-calibrated phylogenies is adding to the evidence that many radiations are recent, dating to the Miocene and Pliocene, with notable examples across different biomes in this Special Issue (Koenen *et al.*, pp. 327–339; Hughes & Atchison, pp. 275–282; Breitkopf *et al.*, pp. 377–389; Spriggs *et al.*, pp. 340–354). For example, Koenen *et al.* (pp. 327–339) present evidence for convergent, late Miocene Amazonian rain forest radiations within the Meliaceae, contemporaneous with other species-rich Amazonian plant clades that also appear to have rapidly diversified around this time (Richardson *et al.*, 2001a; Erkens *et al.*, 2007; Särkinen *et al.*, 2007). It is increasingly apparent that the late Miocene, coinciding with the emergence of much of the world's landscape known today (Potter & Szatmari, 2009) and with the onset of global cooling and increased seasonality, was a pivotal time for diversification of a large fraction of modern plant species diversity (Richardson *et al.*, 2001b; Klak *et al.*, 2004; Arakaki *et al.*, 2011; Hughes *et al.*, 2013; Xing *et al.*, 2014; Koenen *et al.*, pp. 327–339; Bouchenak-Khelladi *et al.*, pp. 313–326). Koenen *et al.* (pp. 327–339) provide a thought provoking discussion of what might account for this pattern and put forward a model of high episodic species turnover. They suggest that the museum model of gradual accumulation of species through time with low extinction needs to be recast as a museum of higher-level taxa and high trait diversity which provided the stock for more recent radiations (Koenen *et al.*, pp. 327–339). Similarly, Spriggs *et al.* (pp. 340–354) and Donoghue & Sanderson (pp. 260–274) home in on depauperate lineages as evidence of species turnover because species-poor lineages are most likely the survivors of much more species-rich clades from the past which have been over-written and obscured by later radiations. This viewpoint of radiations as the counterpoint to, and indeed the outcome, of turnover chimes with fossil evidence suggesting high turnover associated with periods of extreme global climate change during the Cenozoic (e.g. Jaramillo *et al.*, 2010; Xing *et al.*, 2014).

Under a conceptual framework of radiations that emphasizes species diversification over phenotypic disparity (Bouchenak-Khelladi *et al.*, pp. 313–326; Donoghue & Sanderson, pp. 260–274), it is clear that there are many parallel and nested diversification rate shifts – the stacking up of progressive radiations across angiosperms (Smith *et al.*, 2011; Tank *et al.*, pp. 454–467). However, just how many rate shifts there are, and their precise placements on the tree, remain highly debatable. Here there are important questions of phylogenetic scale in relation to taxon sampling, statistical power to estimate rate shifts, and tradeoffs between using sparsely sampled phylogenies of large clades, with their associated difficulties of assigning unsampled diversity, or more densely sampled phylogenies of smaller clades (Smith *et al.*, 2011; Koenen *et al.*, 2013). Under-sampled higher-level trees tend to combine several distinct rate shifts into a single one deeper in the tree and using this method can never hope to accurately locate rate shifts (Koenen *et al.*, 2013; Donoghue & Sanderson, pp. 260–274; Tank *et al.*, pp. 454–467). Even with corrections for incomplete taxon sampling, the locations of rate shifts can still change as sampling increases (Spriggs *et al.*, pp. 340–354). At the other end of the spectrum, densely sampled phylogenies of smaller clades suffer from lack of the wider comparative framework needed for statistically powerful analyses of diversification. Perhaps the greatest insights are likely to come from studies of moderately sized clades of 500 to 1000 (optimistically perhaps a few thousand species) where dense sampling, adequate statistical power and richly detailed trait and geographical datasets are achievable. The lure of

the quest for the perfect phylogeny incorporating near-complete taxon sampling, dense sampling of intraspecific diversity, and robust support over large enough clades to properly elucidate the evolutionary dynamics of diversification at multiple phylogenetic levels (Barraclough & Humphreys, pp. 291–296) appears tantalizingly within reach, but has remained elusive so far.

Why?

Although it has long been suggested that both extrinsic opportunity and intrinsic innovation can be important triggers of radiations (Simpson, 1953), the search for single key innovation or key opportunity explanations has dominated thinking over recent decades. However, very few of the classical single point key innovation explanations for plant radiations have withstood deeper scrutiny (Donoghue & Sanderson, pp. 260–274), prompting a shift towards more complex explanations involving combinations of factors acting synchronously or in sequence (Moore & Donoghue, 2007; Drummond *et al.*, 2012; Wagner *et al.*, 2012; Givnish *et al.*, 2014; Bouchenak-Khelladi *et al.*, pp. 313–326; Donoghue & Sanderson, pp. 260–274). This trend is highlighted by Bouchenak-Khelladi *et al.* (pp. 313–326) and Donoghue & Sanderson (pp. 260–274), who present new conceptual frameworks for discerning combinations of traits and circumstances that together are required for radiation. This is in line with many of the empirical phylogenetic studies in the Special Issue, which home in on sets of intrinsic and extrinsic correlates of radiations. With the blossoming of neontological approaches to investigate these issues, comes the need for new terminology, and a slew of new terms – *confluence*, *synnovation*, *backgrounds*, *triggers*, *modulators*, among others – are proposed here to describe these sequences (Donoghue & Sanderson, pp. 260–274; Bouchenak-Khelladi *et al.*, pp. 313–326).

Alongside this new paradigm for understanding what drives radiations, Bouchenak-Khelladi *et al.* (pp. 313–326) also present one of the first across-clade analyses of radiations and their triggers for three large plant clades: Ericaceae, Poales and Fagales. Adding the Bromeliaceae (Givnish *et al.*, 2014; Donoghue & Sanderson, pp. 260–274) one would hope that general insights about why radiations happen might start to emerge. What does emerge is that, just as for the ubiquity of radiations in terms of *where* they happen, *why* they happen also apparently involves a spectacularly cosmopolitan range of trait combinations as hypothesized triggers of radiation. Furthermore, specific traits do not necessarily have any generalizable effect on diversification (e.g. Chomicki & Renner, pp. 411–424).

How?

To Linder's (2008) questions of the *where*, *when* and *why* of radiations, here we add the much more challenging *how*, that is, what are the evolutionary processes and mechanisms underlying radiations. Of interest here is the new conceptual model of adaptive radiation of Seehausen (pp. 304–312). This model shows how ecologically and phenotypically versatile populations, with highly evolvable mate choice, can rapidly diversify in spatially heterogenous environments with multi-dimensional resource gradients. Seehausen's model, although developed to explain cichlid fish radiations, is of great relevance for understanding plant radiations, given the intriguing, and at first sight surprising, parallels between fish radiations and plant radiations (Seehausen, pp. 304–312). The emergence of genome sequences for cichlids (Brawand *et al.*, 2014) has pointed to an excess of gene duplications and diverse enrichment of the ancestral genome in rapidly radiating cichlid lineages. With their propensities towards genomic obesity and an extensive history of whole genome duplications, genome architecture is likely to have played a central role in driving plant diversification, even if the links between specific whole genome duplication events and accelerated diversification remain controversial (Soltis *et al.*, 2009; Schranz *et al.*, 2012; Tank *et al.*, pp. 454–467).

Equally challenging are questions about how radiations interact, co-exist with each other and influence community assembly, and what are the ecological limits to diversity in this context (Cook *et al.*, pp. 390–400)? One of the most striking features of plant diversity hotspots like the Andes or the Cape Floristic Region is that numerous species-rich radiations across disparate lineages occur superimposed one on top of another (e.g. Linder & Hardy, 2004; Madriñán *et al.*, 2013; Cook *et al.*, pp. 390–400). Disentangling how these multiple sympatric radiations interact with each other in relation to the overall assembly of species-rich plant communities across space and time, especially in highly dynamic environments, is extremely taxing. These questions are tackled by Tanentzap *et al.* (pp. 468–479), using New Zealand alpine radiations to show that early arriving lineages have greater opportunities to radiate than later arrivals, in line with ideas about niche pre-emption on islands (Silvertown *et al.*, 2005).

Conclusions

The geographical and ecological ubiquity of radiations, the multi-episodic nature of plant diversification, and the diversity and complexity of triggers of diversification come across strongly in this Special Issue. This takes us back to the intrinsic evolutionary lability and the ability of flowering plants to repeatedly reinvent themselves time after time using diverse trait innovations and taking advantage of diverse opportunities, that has perhaps been the key to the progressive radiation of the angiosperms (Crepet & Niklas, 2009).

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